

COMPETITION FOR LARVAL FOOD PLANT BETWEEN *DELIAS ARGENTHONA* (FABRICIUS) AND *DELIAS NIGRINA* (FABRICIUS) (LEPIDOPTERA: PIERIDAE) IN COASTAL WALLUM HABITAT IN SOUTHERN QUEENSLAND

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Abstract

In parts of their ranges the mistletoe-feeding pierines *Delias argenthona* (Fabricius) and *D. nigrina* (Fabricius) overlap in time and space and compete for larval food plant. The range of food plants used does not correspond exactly for the two species, which also exhibit different phenologies in a given locality, *D. nigrina* preferring the cooler months of the year. In coastal wallum forest in southern Queensland, larvae of both feed on the mistletoes *Dendrophthoe vitellina* and *Muellerina celastroides* but *Diplatia furcata* is utilised only by *D. argenthona* and *Amyema congener* only by *D. nigrina*. This study demonstrates that, in the presence of a competitor, both *Delias* Hübner species switch their oviposition patterns, laying more of their egg clusters on the mistletoe species not used by the competing species. It is also demonstrated that, in experimental situations, ovipositing females of both species avoid plants carrying egg masses of their own and the competing species and lay preferentially on plants without eggs. It is suggested that in nature the decision to oviposit is made only after a thorough visual assessment of the mistletoe plant and plants bearing eggs are avoided.

Introduction

Larvae of the endemic Australian pierine species *Delias argenthona* (Fabricius) and *D. nigrina* (Fabricius) feed almost exclusively on mistletoes. Braby (2006) recorded *D. argenthona* larvae in Australia as feeding on 12 species in five genera of Loranthaceae, as well as a single record of larvae on *Santalum lanceolatum* (Santalaceae). For *D. nigrina*, Braby (2006) listed 15 species in six genera of Loranthaceae as natural food plants. Mistletoes known to be utilised by both species include *Amyema cambagei*, *A. miquellii*, *Dendrophthoe curvata*, *D. glabrescens*, *D. vitellina* and *Muellerina celastroides*.

Throughout their ranges, which largely overlap in eastern Australia from Cape York to the Victorian-NSW border (Braby 2000), habitat, altitude and phenology frequently segregate *D. argenthona* and *D. nigrina* populations. In southern Queensland *D. argenthona* is most common in the coastal lowlands, where adults are abundant in autumn and spring. It also occurs in moderately dry inland areas but is generally absent from upland areas and from rainforest. Adults of *Delias nigrina*, by contrast, are common in upland rainforest from late spring to late autumn, being absent from these areas in winter. In the coastal lowlands they are most common in winter, seldom appearing before mid autumn. These differences are at least partly attributable to the different effects of temperature on the development and survival of the two species, *D. nigrina* preferring distinctly lower temperatures than *D. argenthona* (Nousala 1979, Braby and Lyonns 2003). In tropical northern Queensland *D. nigrina* is exclusively a montane species,

flying mainly in the winter. *Delias argenthona* is also most commonly found in high country, being replaced on the coast by the tropical *D. mysis* (Fabricius). All recorded food plants of *D. mysis* are also utilised by *D. argenthona* (Braby 2000).

At Currimundi Lake, Caloundra, southern Queensland, there are extensive stands of low mixed *Melaleuca* and *Banksia* forest growing on white sand adjacent to urban development. This is a climax stage of the vegetation complex known as 'wallum' (Coaldrake 1961). Four mistletoe species occur in the area: *Amyema congener*, *Dendrophthoe vitellina*, *Diplatia furcata* and *Muellerina celastroides*, all at moderate to high abundance and infesting mainly the dominant tree species. In this habitat, at different times of the year, *D. argenthona*, *D. nigrina* or both are usually exceedingly common and together utilise all four mistletoe species as larval food plants. However, *Diplatia furcata* is utilised only by *D. argenthona* and *Amyema congener* only by *D. nigrina*.

In 1974, I first noticed that *Delias* herbivory often defoliated clumps of mistletoe in nature, with larval cohorts, sometimes including both species of *Delias*, dying of starvation. Moreover, it was clear that, although there was an apparent hyper abundance of mistletoe, much of the growth was very old and sclerotised and larval survival in captivity on such fodder was invariably poor. Eggs were almost always laid on the freshest growth available. This suggested that, although there was an apparent abundance of food plant, the real amount of high quality food available was often limiting, providing the conditions under which both intra- and interspecific competition could occur.

The central question was, therefore, what might be the effect of interspecific competition on food plant utilisation? To answer this, biweekly censuses were made from February to September 1975 of all *Delias* early stages on mistletoes growing along a standard path of 1.5 km. Adult censuses were also made concurrently. Of the considerable amount of data gathered, the most significant and easily interpreted were provided by the egg censuses and this is reported and analysed below. The eggs of *D. argenthona* and *D. nigrina* are particularly easy to census, being laid in large clusters on their small, discretely clumped food plants. Not only do the eggs of the two species differ in their fine structure, easily seen with a hand lens, but also the two species cluster their eggs in quite different patterns. *Delias argenthona* lays between 15-30 eggs in closely aggregated rows of 2-3 eggs, whereas *D. nigrina* lays from 20-60 eggs in an almost circular pattern with the eggs well spaced.

Between 1982 and 1985, as part of a larger study of reproductive physiology of *Delias* Hübner (Orr 1988), I conducted, within a large outdoor flight cage, a short series of experiments on the response of female *Delias* to the presence of eggs of their own and other species when choosing plants on which to lay. These results are reported here in full.

Area and methods

Field study, 1975

The study area lay mainly along the southern shore of Currimundi Lake (26°28'S, 153°10'E), then a semi-urbanised area with a broad strip of natural growth ranging from 20-50 m wide along its southern boundary (Fig. 1). Dominant trees were *Melaleuca quinquinerva* and *Banksia integrifolia* with some *Casuarina equisetifolia*, all of which supported mistletoes. Crown height of the trees was seldom more than six metres. (The area is still largely intact today, but the trees have grown much taller and many mistletoes have been removed by misguided environmental vigilantes). Within this area, and in several nearby gardens, 33 individual mistletoe plants were located within easy reach (only 5 others were present, beyond reach). A standard sampling path of 1.5 km, including all reachable plants, was established beginning at point 'A' and ending at point 'B' in Fig. 1.

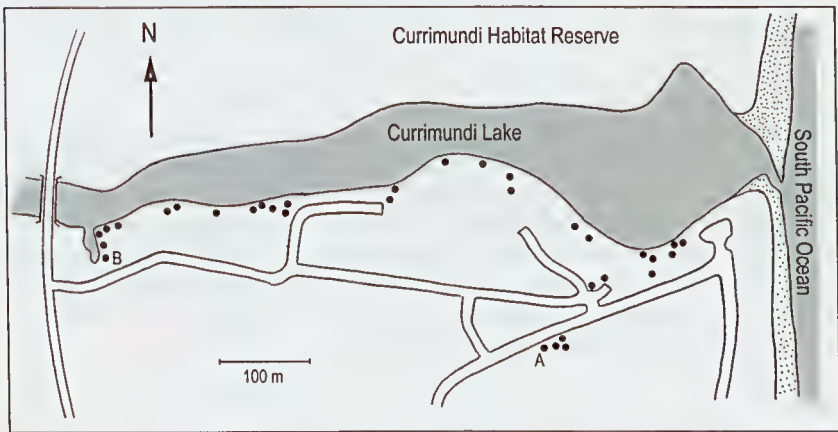


Fig. 1. Map of the study area in 1975 showing location of mistletoe plants (solid circles) relative to Currimundi Lake and major streets. 'A' and 'B' mark the start and finish of the standard transect.

When first located in February 1975, mistletoes were identified to species, numbered and tagged. An estimate was made of the volume of each plant by measuring, with a metre rule, three principle orthogonal axes. The volume was calculated by taking half the mean of these three measurements and calculating the volume of a sphere of this radius. This measurement was correlated quite closely with total foliage and therefore measured the relative amount of food available on each plant.

From 15 February 1975 to 29 September 1975, the plants were examined every 3-4 days for new egg masses. Once located, the eggs in the mass were counted and the mass marked as having been recorded by tying a small twist of fine cotton thread (white for *D. argenthona*, red for *D. nigrina*) to the base of the leaf on which they had been laid. Only new egg batches were recorded during a sampling session. Because the incubation time of eggs of both *Delias* species is about 5 days, this protocol ensured that all *Delias* eggs laid on the sample mistletoes would be recorded once and only once.

Oviposition experiments with captive butterflies, 1982-3

Butterflies were maintained in one of two 4 m x 3 m x 2.5 m outdoor insectaries where they spent their entire lives, having been raised in captivity and introduced to a cage soon after eclosion. As a rule, no more than 5 females were kept in a cage at any time and mostly these were all of one species. During oviposition experiments only one female was allowed in the main cage. On different occasions, 12 individual female *D. argenthona* and 21 individual female *D. nigrina* were presented with three sprigs of fresh *Dendrophthoe vitellina* placed in different corners of the cage. This was done at a time when females were known to be highly gravid and ready to oviposit. Each sprig had approximately 8-12 leaves and, of the three, one bore a single batch of *D. nigrina* eggs and one a single batch of *D. argenthona* eggs, while one (the control) was free of eggs. Often it was necessary to artificially attach an egg mass to the sprig in order to obtain the desired experimental material. The reactions of ovipositing females were noted, especially the first choice of oviposition site. As cut mistletoe retains its turgor for only 2-3 hours, most often the females oviposited only once before the plant had to be replaced and, in this account, only the first oviposition choice of the female was recorded even if a second egg batch was laid.

Results

Oviposition patterns in the field

Mistletoe species were distributed without any apparent pattern along the transect, except for some obvious clumping around thickets of food trees (Fig. 2). Note that Fig. 2 shows the distribution of plants along the path walked, which was far from being a straight line, and hence the relative dispersion of mistletoe plants is somewhat approximated.

Of the 33 plants included in the study, *Amyema congener* and *Dendrophthoe vitellina* were present in almost the same numbers but *D. vitellina* represented, by a small margin, the greater volume of foliage. *Diplatia furcata*, with seven individuals, was present in moderate numbers and *Muellerina celastroides* was uncommon, with only three individuals present (Table 1).

Delias argenthona actively oviposited from February to late May and again from late August to late September, when observations ceased (Fig. 3). *Delias nigrina* actively oviposited from early April until late September, peaking in activity during the winter months (Fig. 3). There were thus about 8 weeks during which both species were abundant and reproductively active. These periods corresponded closely with sightings of adult butterflies.



Fig. 2. Distribution of mistletoe species along the sample path; heights of bars indicate estimated leaf volume. Mistletoe species are as follows: A, *Amyema congener*; D, *Dendrophthoe vitellina*; F, *Diplatia furcata*; M, *Muellerina celastroides*. The spread of individual plants has been exaggerated slightly in places to accommodate lettering.

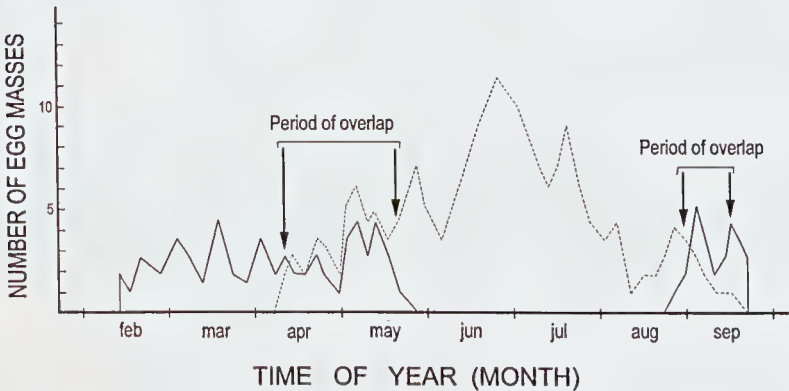


Fig. 3. Phenology of appearance of new egg masses of *D. argenthona* (—) and *D. nigrina* (---) between February and September 1975. Periods of overlap and potential competition are indicated.

The dispersion of eggs on the food plants was complex and undoubtedly was influenced by the availability of fresh growth on each plant, which varied from plant to plant throughout the season. Although it was thought that egg masses of each species were dispersed so as to avoid those of their conspecifics, no simple measurement could demonstrate this conclusively. However, *D. argenthona* and *D. nigrina* showed distinct differences in food plant utilisation: *D. argenthona* never oviposited on *Amyema congener*, whereas *D. nigrina* never oviposited on *Diplatia furcata* (Table 2).

Table 1. Abundance of various mistletoe species and percentage of total foliage volume represented by each species.

Species	number of plants	% of total foliage volume
<i>Muellerina celastroides</i>	3	7.3
<i>Diplatia furcata</i>	7	14.2
<i>Amyema congener</i>	12	34.0
<i>Dendrophthoe vitellina</i>	11	44.5

Table 2. Numbers of egg batches laid by *D. argenthona* and *D. nigrina* on four mistletoe species in the presence or absence of the other *Delias* species. Df, *Diplatia furcata*; Ac, *Amyema congener*; Dv, *Dendrophthoe vitellina*; Mc, *Muellerina celastroides*.

<i>Delias</i> spp.	Df	Ac	Dv	Mc	Total
<i>D. argenthona</i> alone	12	0	58	9	79
<i>D. argenthona</i> : <i>D. nigrina</i> present	31	0	11	3	45
<i>D. nigrina</i> alone	0	67	46	5	118
<i>D. nigrina</i> : <i>D. argenthona</i> present	0	52	9	7	68

In the absence of *D. nigrina*, *D. argenthona* oviposited mainly on *Dendrophthoe vitellina* and the proportion of egg masses on the three food plants used was nearly proportional to the amount of foliage available, with a slight and perhaps insignificant preference for *D. vitellina* (Table 2). However, when *D. nigrina* was present *D. argenthona* switched to using mainly *Diplatia furcata*, the species not attacked by *D. nigrina*. This difference is highly significant (Chi^2 [2df] = 36.9, $p < 0.0001$).

Similarly, *D. nigrina*, in the absence of *D. argenthona*, oviposited almost equally on *Amyema congener* and *Dendrophthoe vitellina*, exhibiting a slight preference for the former in terms of available foliage. However, in the presence of *D. argenthona*, *D. nigrina* oviposited mainly on *Amyema congener*, the species not used by *D. argenthona*. This shift is highly significant (Chi^2 [2df] = 14.75, $p < 0.001$).

Oviposition on the uncommon mistletoe species *Muellerina celastroides* showed no obvious patterns, it being used in moderation by both species. Since *M. celastroides* appeared to be a less favoured plant and was represented by only three individuals, no conclusions can be drawn from the data which, however, have been included in the above analyses.

Oviposition experiments with captive butterflies

Table 3 shows the number of egg masses laid by each *Delias* species on three classes of *Dendrophthoe vitellina* sprig offered: ARG included *D. argenthona* eggs, CONTROL was free of other eggs and NIG included *D. nigrina* eggs.

Table 3. Number of egg masses laid by different captive females on sprigs of mistletoe free of eggs (CONTROL), or carrying an egg mass of either *D. argenthona* (ARG) or *D. nigrina* (NIG).

<i>Delias</i> spp.	ARG	CONTROL	NIG	Total
<i>D. argenthona</i>	2 (17%)	10 (83%)	0	12
<i>D. nigrina</i>	4 (19%)	14 (67%)	3 (14%)	21

For *D. argenthona*, of 12 egg batches produced 10 (83%) were on the control sprig and two batches (17 %) were on sprigs that already bore *D. argenthona* eggs; none was laid on sprigs with *D. nigrina* eggs. The avoidance of sprigs bearing eggs of other females was clearly significant (Chi^2 [1df] = 14.0, $p < 0.001$), but the sample size is too small to show if females avoid eggs of *D. nigrina* more than those of their own species. However, on one occasion in an unrelated study, a female *D. argenthona* laid a second batch of eggs on a plant with *D. nigrina* eggs. Before oviposition she scraped away with her forelegs the *D. nigrina* eggs, which were freshly laid and not adhering firmly to the leaf, before placing her own eggs on another leaf. As this was not part of the choice experiment the result is not included in Table 3.

For *D. nigrina*, a similar avoidance of leaves already bearing eggs was evident, with 14 (67%) of egg batches laid on control sprigs. This is also highly significant (Chi^2 [1df] = 10.57, $p < 0.01$), but there was no evidence to suggest that, when avoiding egg masses already present, females differentiated between eggs of their own species and those of *D. argenthona*.

Discussion

The results clearly show that when both *Delias* species are present, switching occurs in the food plants utilised, with both *D. argenthona* and *D. nigrina* tending to oviposit more on the mistletoe species which each utilises exclusively. From experiments in captivity, it is evident that ovipositing females avoid plants with eggs of their own and other species. It is, however, unclear if heterospecific eggs are more of a deterrent to oviposition than

conspecific eggs but this seems likely to be the case. It is almost certain the butterflies would be able to ascertain the species of eggs present on a plant, as the visual pattern of the egg clusters is very different for the two species. The most probable explanation for the food plant switching observed is that it is a response to visual detection of egg clusters of the competing species on the shared food plants. The oviposition behaviour of *Delias* lends support to this hypothesis; females seldom commit to depositing an egg cluster without having first closely inspected, visually, every fresh leaf on a plant. On the other hand, testing of leaf quality with the ovipositor and/or forelegs is rather perfunctory.

While individual plants varied a good deal in their suitability to sustain larvae, with a few too small to nourish a large cohort and some completely defoliated during the course of the study, there was no evidence to suggest that the switching of *D. argenthona* from *Dendrophthoe vitellina* to *Diplatia furcata*, or of *D. nigrina* from *Amyema congener* to *Dendrophthoe vitellina* when *D. argenthona* finished its season, was related to a change in the quality of the food plants. *Diplatia furcata* is probably an inferior food plant for *D. argenthona*, as larvae reared in captivity on this food develop more slowly and survive less well than those reared on *Dendrophthoe vitellina* (Orr, unpublished observations). In June, many *Dendrophthoe vitellina* plants had been severely eaten by cohorts of both species yet, once *D. argenthona* finished its season, *D. nigrina* still showed a significant switch to this food plant, possibly because of its essentially superior nutritional qualities.

Such examples of interspecific competition are quite rare in nature; much more often we are witness to 'the ghost of competition past' (Connell 1980). The fact that *D. argenthona* and *D. nigrina* are largely allotopic and allochronic means that they can maintain populations which never compete with each other and so seldom come under pressure to diverge ecologically. This is especially true if populations are fairly open, as seems to be the case from mark-release-recapture data (Orr, unpublished data). The abundance of the high-quality mistletoe *Dendrophthoe vitellina* in the coastal wallum seems to provide an unusually rich resource over which they compete intermittently. In the study area, population levels of both *Delias* species regularly reached higher densities than at any other locality I know. Such a situation of an isolated but extremely rich resource is doubtless conducive to competition.

It is interesting to speculate on what might be the competitive relationships among the montane *Delias* of New Guinea. Very often, in a given locality closely related species pairs tend to show different altitudinal preferences (Parsons 1998). However, this does not exclude competition among members of different species groups. In two weeks in December 1973, at one locality on Mount Kaindi in Morobe Province, I collected 12 species, at least half of which were abundant and only three of which could be considered rare. Even

more impressively, during December 1973 and January 1974, the total number of species I collected on the same mountain at different altitudes above 1000 m was 21, about a third of the known *Delias* fauna for mainland Papua New Guinea. Ecological segregation under these circumstances must surely be a complex process.

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